Pre-migratory “fattening” usually involves more than the deposition of fat alone

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Viewpoint

Pre-migratory "fattening" usually involves more than the deposition of fat alone

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Most ringers are actively pursuing the study of bird migration, either straightforwardly through the description of birds' paths through space and time, or more indirectly, by describing the physiological changes of birds, such as increases in body mass, as they prepare for their flights. Long-distance flights over inhospitable habitat necessitate the storage of sufficient nutrient reserves to keep the birds going throughout the envisaged travel periods without the need to refuel. Here I want to respond to two recent papers in *Ringing & Migration* on pre-migratory body mass changes in two passerine species (Karlsson *et al.* 1988 and Banks *et al.* 1989). In both papers the authors failed to attribute interesting place- or time-related differences in the relationships between visual fat score and body mass, to differences in fat-free mass.

Karlsson *et al.* (1988) interpret a difference in the fat score — body mass relationship between two populations of migrating Robins *Erithacus rubecula* with equal wing lengths, as probably a result of adaptive pre-migratory water loss. Banks *et al.* (1989) acknowledge that part of the difference between the fat score — body mass relationship in Snow Buntings *Plectrophenax nivalis* in midwinter, compared to spring migration may be due to increases in breast muscle mass (*cf.* Fry *et al.* 1972, Marsh 1984). However, they attribute most of the 17% difference (*i.e.* 6/36 x 100% at fat score 4, their Fig. 5), to changes in water content (*i.e.* to adaptive premigratory dehydration) or changes in the distribution of stored fat within the buntings' bodies (relatively less subcutaneous fat in spring resulting in a higher body mass per fat score than in midwinter). Based on a series of rather recent findings, I believe that in both cases the differences are likely to be only due to changes in total fat-free mass (which includes muscle mass as one of the changing components). The apparent reluctance of both groups of authors to consider changes in total fat-free mass as the reason for the discrepancies between different fat score — body mass relationships, may represent a legacy of the Odum *et al.* (1964) "doctrine", which states that all premigratory mass changes (in passerines) are due to changes in fat load (see for example reviews by Blem 1980, 1990, Lindström 1986). This is now known not to be true in many bird species, including passerines.

Adding on to earlier work on Canada Geese *Branta canadensis* (McLandress & Raveling 1981), several recent studies of body composition changes in waders (Charadrii) before spring migration have shown that between 20% and 50% of the body mass gains are attributable to increases in fat-free mass (Davidson & Evans 1986, Piersma & van Brederode 1990, Piersma & Jukema 1990, review in Zwarts *et al.* 1990). For Garden Warblers *Sylvia borin* during autumn migration, Biebach (1990) found that a one gram change in total body mass corresponds to a 0.7 g gain in fat mass (*i.e.* 30% of the gain is fat-free mass, just as in waders). Because the energetic yield of fat (*ca.* 40 kJ/g) is about eight times higher than the energetic yield of fat-free tissue (*ca.* 5 kJ/g, assuming it mainly consist of "wet" muscle protein: 70% water and 30% dry protein), 90% of the energy gain during the

pre-migratory "fattening" episode comes in the form of fat, even in the case where only 50% of the deposited mass is fat. Why would migrant birds store such a large and heavy protein reserve when the energetic yield during flight will be so small?

In the case of Bar-tailed Godwits *Limosa lapponica*, 50% of the body mass gains in spring consisted of fat-free body tissue. Only 15% (in the Dutch Wadden Sea) to 40% (on the Banc d'Arguin, Mauritania) of the increase in fat-free mass could be accounted for by the mass increase of the breast muscles (Piersma & Jukema 1990). Hypertrophy was clearly going on in most parts of the body. The body mass lost by Bar-tailed Godwits during their flight from Mauritania to The Netherlands also consisted of about 50% of fat-free body mass. Only 20% of this mass loss could be accounted for by a decrease in the mass of the breast muscles. Although Pennycuick's (1978) argument from aerodynamic design might explain the loss of breast muscle mass during the 4300 km long flight, other non-fat parts of the body lost mass too, and other (purely physiological) mechanisms must therefore additionally play a rôle. Since migrants in flight do not normally ingest any food for one or more days, their mass loss can be compared to the well studied mass loss in starving animals (Deerenberg 1988, see *e.g.* Le Maho *et al.* 1981. Cherel & Le Maho 1985, Cherel *et al.* 1987). In domestic geese *Anser domesticus*, 58% of the total mass loss during a prolonged fast of more than 40 days was due to fat loss and 34% to the loss of muscle tissue (Le Maho *et al.* 1981). Fat and muscle protein contributed respectively 94% and 6% of the total energy expenditure during the fast, values which are close to the values (*ca.* 90% and 10%) for migrant Bar-tailed Godwits during a 4300 km long flight (Piersma & Jukema 1990). This suggests that the loss of fat-free tissue during a long-distance flight can be explained by the minimum requirement for protein for repair (and after replacement: as fuel) in a fasting but hard working organism. From a physiological point of view, long-distance migration may be considered as a very rapid starvation process.

For this reason there is perhaps nothing surprising in the considerable increases in the low-yield gains in fat-free mass before long-distance flights: it represents storage of a supply of fresh "parts to keep the engine going". At take-off this labile protein forms part of the motor itself, a part which can be re-used however when in the course of flight the fat loads decrease and the need for motor-power becomes smaller. Indeed, one wonders why in some careful and detailed studies authors have failed to recognize (Marsh 1983) or discuss (Johnson *et al.* 1989) the overall change in fat-free mass. Partially this may be due to the type of statistical analyses employed (for a discussion see Piersma & Jukema 1990), but I fear it is also (probably unconsciously) due to a restricted "scientific search image" resulting from the Odum *et al.* doctrine. For example, Fig. 2 of Marsh (1983) in fact indicates that increases in the mass of carcasses (without breast muscles!) of Gray Catbirds *Dumetella carolinensis* can not fully be explained by the increase in fat mass.

But what about the explanations which Karlsson *et al.* and Banks *et al.* did put forward to account for the discrepancies between different fat score — body mass relationships? How and where fat is stored is obviously an adaptive phenomenon (see Pond 1978). A selective subcutaneous deposition of fat in the cold winter months to provide an insulative layer, provides an attractive hypothesis to explain why Snow Buntings in midwinter show lower body masses at equal fat loads) than in spring (Banks *et al.* 1989). Detailed body composition analyses are required to find out. The other explanation, the adaptive pre-migratory dehydration hypothesis, is empirically poorly supported and theoretically unlikely. Davidson (1984) mentions a single Sanderling *Calidris alba*, and there is Fogden's (1972) study of exceptionally dehydrated Reed Warblers

Acrocephalus scirpaceus during a dry spring in Uganda. In contrast, I have not yet found any evidence for dehydration in the analyses of hundreds of wader and grebe carcasses. In fact, most detected small water losses appear to be due to methodological shortcomings (Piersma & van Brederode 1990). Child & Marshall (1970) emphasize the constancy of body water as a percentage of fat-free mass in passerines, and several physiological (Hart & Berger 1972, Biesel & Nachtigall 1987) and ecological (Biebach 1990) studies stress that (physiological limits to) water loss may often constrain flight duration.

Serious bird ringers have much to contribute to this discussion. Co-operation with laboratory biologists would allow body composition analyses of unavoidable catching casualties to be put to a good use to elucidate the poorly understood relationships between visual fat score and total body mass. Apart from getting to grips with what a subjective visual fat score actually means in terms of "hard currency" (g fat or kJ), much valuable new data may so become available describing where, before which flights, in which species and to what extent, protein in addition to fat is stored before take-off.

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